Vol. XII. *April, 1907.* *No. 5.*

BIOLOGICAL BULLETIN

NOTE ON THE CHROMOSOME-GROUPS OF METAPODIUS AND BANASA.[1]

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I am led to publish the following preliminary note lest confusion should arise from the peculiar relations of the chromosomes in *Banasa calva* described in the second of my "Studies on Chromosomes,"[2] which have now, I believe, become explicable as a result of additional studies on *Banasa*, but more especially on the genus *Metapodius*. At the time these relations were described in *Banasa calva* they appeared to be unique in that both an unpaired chromosome (apparently an "accessory" chromosome) and a typical pair of unequal idiochromosomes are present in the same species, and four classes of spermatozoa are accordingly formed. The coexistence of these two forms of chromosomes in the same individual has already been considered by more than one writer as a serious difficulty in the way of my general interpretation of the significance of these chromosomes in sex-production. It was (and is) my view that the "accessory" chromosome is the homologue of the large idiochromosome and like the latter is distinctive of the female-producing spermatozoa. It seemed, no doubt, an obstacle to this view that an unpaired or heterotropic chromosome should coexist with a pair of idiochromosomes in the same species, and that it should in one class of spermatozoa be associated with a large idiochromosome, in another class with a small one. With the material at my command (which included only two testes from the Paulmier collection) I was not in a position to

[1] The material on which the observations were made is part of a series procured in the course of an extended collecting trip to the south and west in the summer of 1906, the cost of which was in part defrayed by a grant from the Carnegie Institution of Washington. The results will be published in a more extended form hereafter.

[2] *Journ. Exp. Zool.* II., 4, 1905.

meet this difficulty or to give an adequate explanation of the facts; and for a time, I even suspected that the material might be pathological. Recently, however, I have found a similar, though not quite identical, condition in a species of *Metapodius*, and have been able to study the facts more thoroughly. In this form, too, an unpaired chromosome coexists with a typical pair of idiochromosomes (and a pair of *m*-chromosomes as well); but the facts clearly show that it is not of the same nature as the "accessory" or "heterotropic" chromosome of the usual type, and is without constant relation to sex-production. The idiochromosomes show the usual relation, the large one passing to the female producing pole and the small one to the male-producing pole. A comparison of different individuals shows beyond doubt that the unpaired chromosome may be either present or absent in either the male or female, and hence is without significance in sex-production. It is in fact a kind of supernumerary chromosome, which I shall designate as the "*s*-chromosome" in order to distinguish it from the odd sex-chromosome of the usual type — variously known as the "accessory chromosome" (McClung), "heterotropic chromosome" (Wilson), or "monosome" (Montgomery).

1. Metapodius terminalis Dall.[1]

The present account will give only the facts that bear directly on the case of *Banasa calva*. The genus *Metapodius* is, I believe,

[1] The following description will be found to differ widely from that given for the same species by Montgomery (*Trans. Am. Phil. Soc.*, N. S., XXI., 3, 1906), who states that there are 21 spermatogonial chromosomes and an ordinary large odd chromosome in the second division. Professor Montgomery has kindly sent me some of his own material, collected in Pennsylvania, a study of which has convinced me of the correctness of his account. My own material is from New Jersey, North Carolina, South Carolina, Georgia and Ohio; and there can be no doubt of the identification since every original specimen is in my possession (as is the case with all my new material). Through the courtesy of Dr. Uhler I have been enabled to compare these specimens with those in his collection (with which they exactly agree); and they have also been examined by several competent hemipterists, including Mr. Otto Heidemann, of Washington, and Mr. H. G. Barber, of New York, and pronounced by them to be typical *terminalis*. As will be shown, different individuals among these specimens show constant and characteristic differences in the chromosome-groups; but none show less than 22 chromosomes, and none possess a large odd chromosome. The same is true of *M. femoratus* Fab., and *M. granulosus* Dall., both of which, like *terminalis*, possess a typical pair of idiochromosomes. This contradic-

in a somewhat plastic condition as regards the chromosomes, and presents certain variations in the number of the larger chromosomes that need not here be described, since they do not affect the relations to be considered. Alone among all the Coreidæ thus far examined, the three species of *Metapodius* possess a typical pair of idiochromosomes along with a typical pair of *m*-chromosomes — a fact which proves the validity of the distinction between these two forms of chromosomes drawn in my second study. The idiochromosomes are distinctly, though not greatly, unequal in size; and as usual among the Hemiptera, they remain separate as univalents in the first maturation division, but conjugate at the end of this division to form an unequal bivalent. In the greater number of individuals (which may be classed together as "Type A") the first division shows 13 chromosomes (Fig. 1, *b*) and the second 12. In the most usual arrangement the two idiochromosomes (*I* and *i*) lie in the first division not far apart, outside an irregular ring formed of nine larger bivalents, in the position typical of the odd chromosome in other coreids. Near the center of the ring lies a very small *m*-chromosome bivalent (*m*), which as in so many other cases is formed in the late prophases by conjugation of its two members. The thirteenth chromosome is the small unpaired univalent *s*-chromosome (*s*) which divides like all the others in the first division but passes undivided to one pole in the second division. In three of the seven males I have, this chromosome is of the same size as the *m*-chromosomes. In two individuals of the same type it is somewhat larger, though markedly smaller than the large bivalents. In the remaining two males (which constitute "Type B") the *s*-chromosome is wanting in all the cells, whether spermatogonia or spermatocytes. In these individuals the first spermatocyte division uniformly shows 12 chromosomes (Fig. 1, *e*) and the second 11, the grouping being otherwise more or less nearly similar to that in the first type.

tion probably cannot now be resolved, since the original specimens of Montgomery's material are not in existence. I think it probable that two different species have been under observation, and there is some reason to suspect that Montgomery's material may have been *Euthoctha galeator*. This case illustrates the extreme importance, in work of this kind, of preserving every individual from which cytological material is taken.

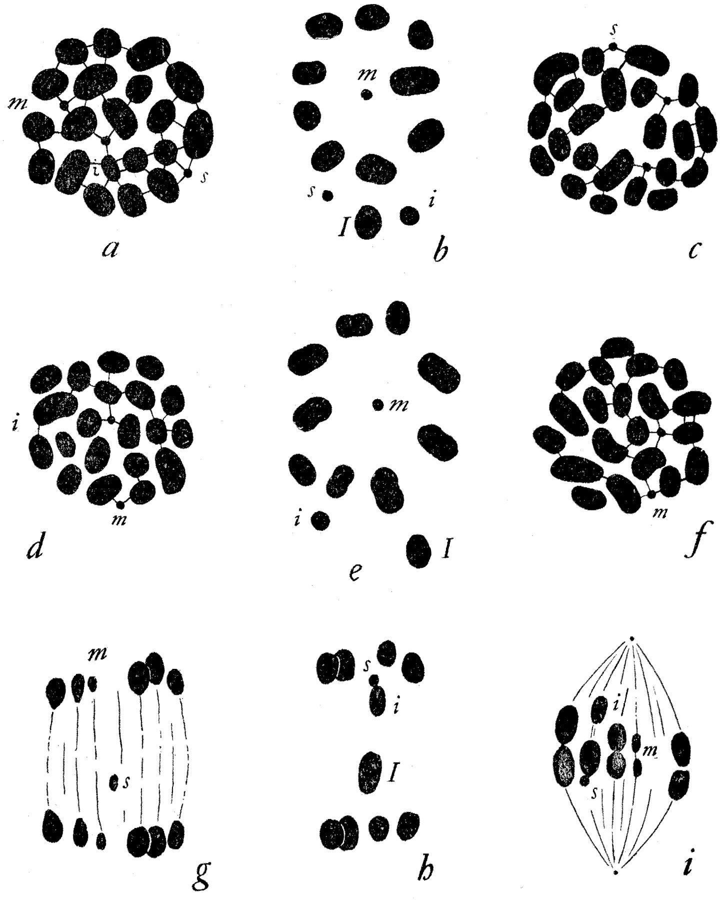

FIG. 1. *Metapodius terminalis.*[1] *a*, polar view, spermatogonial group, Type A; *b*, first maturation-division, Type A; *c*, female, Type A (probably a young follicle cell); *d*, spermatogonial group, Type B; *e*, first spermatocyte-division, Type B; *f*, female group, Type B; *g*, second division, Type A, showing *s*-chromosome free (the idiochromosomes do not appear in the plane of section); *h*, second division in side-view, *s*-chromosome coupled with small idiochromosome; *i*, second division, *s*-chromosome coupled with the large idiochromosome. (Fig. *a* is from a specimen taken at Madison, N. J.; *b*, *g*, *h*, *i*, from one individual from Charleston, S. C.; *c*, *e*, and *f* from Raleigh, N. C.; *d*, from Mansfield, Ohio. A second male of Type B was taken at Raleigh, N, C., from the same catalpa tree with an individual of Type A.)

[1] The enlargement is 3700 diameters — somewhat less than that of the figures in my preceding papers. The figures are all from camera drawings and are not schematized, except that in Fig. 1, *g*, one pair of the chromosomes has been slightly displaced in order to show the *m*-chromosomes more clearly. No attempt is made to show details of the achromatic spindles. In all the figures *I* denotes the large idiochromosome, *i*, the small one, *m* the *m*-chromosome, and *s* the *s*-chromosome. (The latter not to be distinguished from the *m*-chromosomes in *a* and *c*.)

When the *s*-chromosome is present it sometimes (in about 20 per cent. of the cases tabulated) lies free — *i. e.*, not connected with any other in either division — and after dividing in the first division, passes undivided to one pole in the second (Fig. 1, *g*). *In most cases it is in the second division attached to one or the other of the idiochromosomes and passes with it, undivided, to one pole* (Fig. 1, *h*, 1, *i*). In either case one pole receives 11 chromosomes and one 12, as may clearly be seen in polar views of the late anaphases which show both daughter-groups of chromosomes in the same spindle. Four classes of spermatozoa are accordingly formed in this type, which correspond to those described in *Banasa calva.* Designating the ordinary chromosomes or "allosomes" as "*O*," the large and small idiochromosomes respectively as "*I*" and "*i*," the *m*-chromosome as "*m*" and the *s*-chromosome as "*s*" the classes are as follows:

(1) $9\,O + I + m + s = 12,$

(2) $9\,O + I + m = 11,$

(3) $9\,O + i + m + s = 12,$

(4) $9\,O + i + m = 11.$

So far this is identical with the conditions described in *Banasa calva* except that in the latter case the unpaired chromosome fails to divide in the first division but divides in the second, while the reverse condition obtains in *Metapodius.* But there is now an important difference to consider which involves the most interesting phenomenon that occurs in this form. In *Banasa calva* the four classes are equal in number. In *Metapodius*, at least in certain individuals, this is not the case; for the *s*-chromosome shows a marked tendency to couple with the small idiochromosome rather than the large, which produces an excess of spermatozoa in which these two chromosomes are associated. It is somewhat difficult to secure adequate data, since the nature of the coupling can, as a rule, only be determined with certainty in side views of the middle anaphases. Out of 34 clear cases (taken from two individuals) the *s*-chromosome is coupled with the small idiochromosome in 24 and with the large in 10 — *i. e.*, in about 70 and 30 per cent. respectively, a ratio which may very likely be somewhat altered with a larger series of data. Of the four classes, accordingly, 2 and 3 are more numerous than 1 or 4.

Turning now to the spermatogonia, we find an accurate correlation between the spermatogonial chromosome-groups and those of the maturation divisions. In all cases there are 18 equally paired larger chromosomes, an unequal pair of idiochromosomes and a very small pair of *m*-chromosomes; and these 22 alone are present in the individuals of Type B (Fig. 1, *d*). In those of Type A an *s*-chromosome is present in addition, making 23 in all (Fig. 1, *a*). In three of the five males of this type, as stated above, the *s*-chromosome is no larger than the *m*-chromosomes, and the spermatogonia correspondingly show 20 large and three very small chromosomes. In the remaining two individuals of this type the *s*-chromosome is considerably larger than the *m*-chromosomes, both in the maturation-divisions and in the spermatogonia. The spermatogonia of these individuals seem therefore, at first sight, to show 21 large chromosomes and two small. In Type B, which have but 22 chromosomes, the first maturation-division shows but 12 chromosomes, the second 11; and only two classes of spermatozoa are formed, which correspond to Classes 2 and 4 of Type A.

The foregoing data, when compared with the conditions found in the female, give a decisive result regarding the relation of these chromosomes to sex-production. If the unpaired *s*-chromosome were of the same nature as the odd or "accessory" chromosome of other coreids we should expect to find one such chromosome in the male and two in the female; and since males and females alike possess in addition two small *m*-chromosomes the males should show three small chromosomes and the females four. Such however is not the case. In both sexes there are individuals that possess three small chromosomes (Fig. 1, *a*, 1, *c*) and others that possess but two (Fig. 1, *d*, 1, *f*). Evidently therefore the *s*-chromosome is indifferent as regards the sex-characters. On the other hand, close study of the larger chromosomes shows the same relations as those observed in other forms that possess unequal idiochromosomes. In the female groups all are equally paired. In the male all are thus paired save two, one of which is evidently the small idiochromosome.[1]

[1] This fact is not always readily made out, since the small idiochromosome is not very markedly smaller than the others; but I am sure of the observation, and the fact was determined in many spermatogonial groups long before I suspected the presence of a pair of idiochromosomes in this genus.

The usual conclusion follows that spermatozoa containing the large idiochromosome produce females and those containing the small one produce males. It is equally clear that the *s*-chromosome, though unpaired and hence a heterotropic chromosome in behavior, is not physiologically comparable to an odd or "accessory" chromosome of the usual type.

The numerical relations between Types A and B are interesting. Since in maturation the *s*-chromosome couples more frequently with the small idiochromosome (which is confined to the male) we should expect to find the *s*-chromosome in a majority of the males and in a minority of the females; and such is indeed the case in the 12 individuals that have been examined. Of the seven males, five are of Type A and two of Type B — a ratio that happens to be nearly identical with that shown in the coupling. Of the five females on the other hand, only one is of Type A (with three small chromosomes, Fig. 1, *c*),[1] while four are of Type B (Fig. 1, *f*). The number of individuals is of course too small to give an accurate result; but as far as they go the facts are in conformity with the expectation created by the mode of coupling in the spermatogenesis.[2]

Banasa.

The remarkable relations observed in *Metapodius terminalis* probably give the explanation of those I formerly described in *Banasa calva*, though I am not yet in a position to prove this positively. I have now new material of this genus from individuals ranging from New England to Arizona, and comprising both of the more frequent species, *B. calva* and *B. dimidiata*.[3] All

[1] This individual differs from all the others in having 22 instead of 20 large chromosomes, or 25 in all. I have found a similar variation in the number of larger chromosomes in different individuals of two other species of the genus (*M. femoratus* and *M. granulosus*) as will be described hereafter. These variations appear to have no constant relation to the presence or absence of the *s*-chromosome and hence do not affect the questions here under consideration.

[2] Besides the two types of males and females described above we should expect to find a third type in each sex containing two *m*-chromosomes and two *s*-chromosomes. Such forms have not yet come under my observation, and it is possible that gametes containing both these forms of chromosomes are infertile towards each other.

[3] I am indebted to the well known hemipterist Mr. E. P. Van Duzee, of Buffalo, for the identification of these and many other species.

the new material of *calva* differs from the Long Island material that I formerly described in the *absence of the small unpaired or heterotropic chromosome*, though in every other detail they are identical. To facilitate the comparison I give three new figures from the Long Island material (which, as above stated, includes only two slides from the Paulmier collection). The first division here always shows 15 chromosomes (Fig. 2, *a*) of which two, the unpaired chromosome and the small idiochromosome, are much smaller than the others. Owing to the passage of the unpaired chromosome to one pole without division in the first maturation division the secondary spermatocytes are of two types, showing respectively 14 and 13 chromosomes (Figs. 2, *b*, 2, *c*) — a relation shown with perfect clearness in a large number of cells. In all my new material on the other hand (from New York, Ohio, Colorado and New Mexico) the chromosome groups are exactly similar to those of the Long Island form except that the small unpaired chromosome is missing. The first division accordingly always shows 14 chromosomes instead of 15, of which one (the small idiochromosome) is smaller than the others (Fig. 2, *d*). The second division always shows 13 chromosomes, (Fig. 2, *e*) of which one is a typical idiochromosome-bivalent; and in the ensuing division all the spermatids receive 13 chromosomes, half receiving the small idiochromosome and half the large. Both the spermatogonial and the ovarian groups accordingly show 26 chromosomes, the small idiochromosome being present in the male only (Fig. 2, *f*). In every respect, therefore, these individuals show the typical pentatomid relations, and agree with Type B of *Metapodius*.

Banasa dimidiata agrees essentially with this except that to my astonishment the number of chromosomes was found to be much smaller, namely, in the spermatogonia 16 (Fig. 2, *j*), in the first division nine (Fig. 2, *g*), and in the second eight (Fig. 2, *h*). It is noteworthy that these two species, which are so closely similar as sometimes to have been confused by systematists, should differ so widely in the number of chromosomes.

The difference between the material from Long Island, labeled "*Banasa calva*," and my own at first led of course to the suspicion that an erroneous identification was at fault; and this is

indeed possible since the Paulmier slides were not accompanied by the original specimens. But the exact similarity of the two forms in every respect apart from the unpaired chromosome, and my failure to find any other similar form in an examination of nearly all the species of Pentatomidæ that might be confused with this species, leads me to believe that the case of *Banasa*

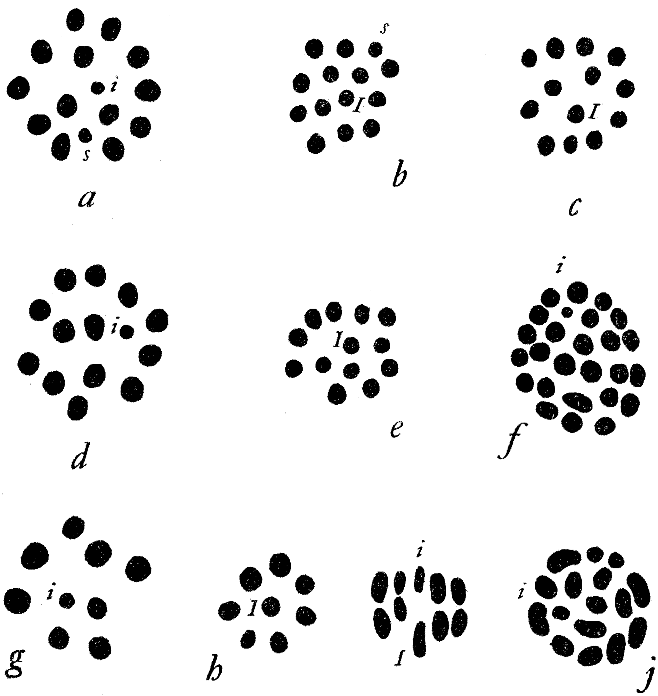

FIG. 2. *Banasa.* (*a–f*, *B. calva*, *g–j*, *B. dimidiata.*) *a*, Long Island form (Paulmier), first spermatocyte-division; *b*, 14-chromosome type of second division; *c*, 13-chromosome type, from the same cyst; *d*, western form (Colorado), first spermatocyte-division; *e*, second division of same; *f*, spermatogonial division; *g*, *B. dimidiata*, first division; *h*, second division, polar view; *i*, side view of same; *j*, spermatogonial group. (In *a* it is impossible to distinguish between the *s*-chromosome and the small idiochromosome.)

calva is probably similar to that of *Metapodius terminalis*, the Long Island form being of one type (corresponding to Type A of *Metapodius*, with an unpaired *s*-chromosome) and the others of the other type (corresponding to Type B of *Metapodius*). In *Metapodius* the two types occur side by side in the same locality;

and the same should be true of the Long Island *Banasa calva* if the two cases are really alike. But this question can only be settled with additional material. All the individuals from western New York (Buffalo) and further west are of Type B. It therefore seems not improbable that one of the types has been lost in the western forms, or conversely, that Type A has been added to B in Long Island, perhaps in a local colony or variety.

Comment.

The strong support lent by the foregoing facts to the general theory of the individuality — or, as I should prefer to say, the genetic identity — of the chromosomes is so obvious as hardly to require comment. I will here only call attention to the interest of the coupling of the *s*-chromosome with one of the idiochromosomes in *Metapodius*. This phenomenon is doubtless comparable in a general way to the coupling of the true odd or "accessory" chromosome with one of the ordinary bivalents first briefly recorded by Sinéty[1] in the Phasmidæ, and carefully studied in several of the grasshoppers (in some of which the facts are more complicated) by McClung[2] who has given an interesting discussion of the subject. I have observed chromosome-couplings in four families of the Hemiptera heteroptera and believe the phenomenon will be found to be of wide occurrence in the insects, and perhaps in other animals. It seems well within the bounds of possibility that such chromosome-couplings may give the physical basis of certain forms of correlation in heredity. If the chromosomes embody the primary factors of heredity (the working hypothesis upon which I am proceeding in these studies), it must no doubt be assumed that each chromosome contains the determinants of many characters; and the association of such determinants in the same chromosome may imply the constant correlation of the corresponding characters in heredity. But in addition to this, certain correlations, such as are observed in some forms of hybrids, might also be a result of a more or less pronounced tendency of certain chromosomes to cohere in a definite way, so as to be more frequently or even invariably

[1] *La Cellule*, XIX., 1901–1902.

[2] Biol. Bull., IX., 5, October, 1905.

associated in the germ-cells. In the case of *Metapodius* such a tendency is shown in the more frequent coupling of the *s*-chromosome with the small idiochromosome, which leads to its more frequent passage to the male-producing pole, and hence to its more frequent appearance in the male. This reminds us of certain crosses of Lepidoptera observed by Standfuss,[1] and more recently by Doncaster and Raynor,[1] in which there is a tendency for a particular set of specific or varietal characters to appear more frequently in one sex than the other. Thus, in *Abraxas*, as reported by the last named observers, after crossing the original form (*A. grossulariata*) with an albinistic variety (*lacticolor*) to which it is dominant, the cross ♂ DR × ♀ RR gives both sexes of both forms, but the reverse cross ♀ DR × ♂ RR results in a sharp separation of the sexes of the two forms, all the resulting males being DR and the females RR. This, as the authors show, may be explained by the assumptions, first, that the sex borne by the egg is uniformly dominant (as appears to be the case in the Hemiptera) and second that the dominant somatic character (*i. e.*, the *grossulariata* pigmentation) uniformly couples with the male character in the egg while in the spermatozoon no coupling occurs. Such a chromosome-coupling as that observed in *Metapodius terminalis* gives a very definite basis for the possible explanation of couplings of the sexual characters with specific or varietal ones; and it seems possible that we may in this direction find a means of testing decisively the whole chromosome-theory of heredity. In the case of *Metapodius* I have not thus far been able to find any constant differences between individuals of Types A and B; but only the external characters are available for examination. I hope hereafter to examine this question more thoroughly, both in *Metapodius* and in *Banasa*.

Zoölogical Laboratory, Columbia University,
February 4, 1907.

[1] See Castle, *Bull. Mus. Comp. Zool.*, XL., 4, 1903.
[2] *Proc. Zool. Soc. London*, June 7, 1906.